CONCEPTS FOR ANALYSIS OF INTERGENOTYPIC COMPETITION
IN FOREST TREES

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Abstract.---Area Potentially Available (APA), an index of
individual-tree competitive status or available growing space, is
adapted for use in the analysis of growth response to
inter-genotypic competition in genetic field tests. The approach
allows geneticists to detect differential response to competition
from neighboring trees that vary in size and distance as well as
genetic identity. Methods for detecting interactions between
genetic entities in response to competition are presented. Data
from a loblolly pine progeny test planted in a Nelder's Wheel
design are used to illustrate the approach.

INTRODUCTION

Competition between trees is universally assumed to operate in closed
stands of forest trees. Clements et al. (1929), in a review of the early
history of competition, noted that foresters were among the first to reco
competitive effects and to attempt to control competition for commercial
benefits through thinning practices. Foresters today regulate inter-tree
competition within forest stands to attain full utilization of forest sites
and to shape the diameter distribution and form of crop trees.

Competition between crop plants is also of vital concern to agronomists,
for they have discovered that the highest yields per acre are generally
attained when the competition between plants is high (Donald, 1961). Crop
breeders recognize that modern crop varieties must have the ability to grow
under extreme density stress, and they have adjusted their selection,
breeding, testing, and deployment techniques accordingly.

In tree improvement programs, much less attention has been given to
competition -- either as a source of improving per acre yields or as a
possible source of error in selection, breeding, and testing. Generally,
forest geneticists select outstanding individual trees and test their field tests
replicated either in single-tree plots, row plots of 2-8 trees, or in small
rectangular or square plots of 4 to 64 trees. The spacing between trees is
generally held constant and wide.

In such tests, the various progenies generally exhibit different growth
rates very early -- long before competition between trees can fully develop
-- and therefore these growth rate differences do not represent differential

response to competition from neighboring trees. Nevertheless, the faster growing progenies do gain a competitive advantage over their slower growing neighbors because they capture a larger share of the site before competition develops. However, progenies selected for vigorous pre-competition growth may not grow well after competition fully develops and neighboring trees begin to compete for limited light, water, and nutrients.

If progenies differ in their response to competition from neighboring trees, then early evaluation of progeny performance could lead to errors in selection, breeding, and deployment of genetic material in operational plantings where competition is unavoidable as well as desirable for most of the commercial rotation. Moreover, if differences between progenies in their response to competition do exist, it is conceivable that geneticists could exploit such differences for commercial advantage.

Considerations such as these raise fundamental questions that can only be answered through experimentation. One approach, often used in crops, is to carefully design competition experiments wherein large plots of single and mixed progenies are established and grown through rotation age. The yields on a per acre basis are then analysed using an adaptation of the analysis for a diallel mating design (Willey and Heath 1969, Mead 1979). This and similar approaches have occasionally been used in forest trees, but only for seedling experiments (Adams et al. 1973, Adams 1980, Cannell 1982, Tauer 1975, Snyder and Allen 1971, and Wearstler 1980).

A less common approach is based on individual-plant competition experiments wherein the number, spatial pattern, and genotype of competing plants is systematically varied to create competitive situations of various types. Growth data are then analyzed using some form of a competition index designed to quantify the competitive situation under which the individual plant responded (Mead 1968, 1979, Willey and Heath 1969).

Most progeny tests, although not designed as individual-tree competition experiments, exhibit many of the features of such experiments. The complex mixtures of genetic entities combined with their differential growth and survival rates before competition create a variety of competitive situations. Once competition begins and growth data are collected in these tests, it should be possible to extract information regarding the response of individual trees to competition from neighboring trees, and to identify those situations in which the genetics of the subject tree or its competitors is a factor in that response.

Concepts and methods are developed in this paper that may allow geneticists to extract such information from genetic field tests. The application of the proposed methods is illustrated with data from a complex genetic field test in loblolly pine (Pinus taeda L.).

METHODS

The fundamental problem in assessing individual-tree response to competition is the development of an index of local density in the neighborhood of an individual tree. Such an index should properly account for the size of the subject tree and the size and spatial pattern of neighboring trees; and it should both reflect the current competitive status of the

subject tree and changes in that status over time. Fortunately, such ani
exists in the form of the APA (Area Potentially Available) index first
introduced by Brown (1965) and later modified by Moore et al. (1973) anda
by Mead (1965).

The APA index.--The APA index is defined as the area of an irregular polyg
constructed around a subject tree. The polygon is formed by intersecting
lines (influence lines) that are located between and perpendicular to the
lines connecting the subject tree and each of its competitors. The area o
the polygon around a subject tree represents the "relative growing space"
"competition status index" of the subject tree within the stand as limited'
its neighbors. This area is mutually exclusive to that of any other tree,
the sum of the areas for all polygons represents the total area utilized b
the stand.

The APA index has recently been compared with several other competit
indices by Daniels (1981), who concluded that the APA index was superior
all those tested for predicting future basal area growth in a long-term
loblolly pine spacing trial. A FORTRAN computer program written by Daniel
(1981), called COMP5, was enhanced by the present authors for use in genetic
field trials with any arbitrary spatial design and genetic structure.
Basically, the enhancements to COMP5 included: (1) additional code to keep
with the genetic identity of all trees, and (2) the addition of a new index
relative influence (RI), useful in detecting genetic interactions.

Computation of the APA index: program COMPAPA.--The program initiates a sear
for influential competitors around each subject tree; assembles a prospectiv
list of those trees which could influence the construction of the subject
tree's polygon; computes all possible intersections of each competitor's •
influence lines with one another; and then constructs the polygon using a
minimum subset of competitors. Further details regarding the methods used
appear in Daniels (1981), and in the program itself which is available on
request.

In this study relative basal area was used as the weighting factor to
locate the influence lines between the subject tree and each competitor (Moor
et al. 1973), which is computed as:

$$LP = \frac{D_S^2}{D_S^2 + D_C^2} \times L$$

where   LP = the distance from the subject tree to the competitor's
             line of influence,

        L = the distance from the subject tree to competitor,

        D_S = d.b.h. of subject tree (in inches), and

        D_C = d.b.h. of competitor (in inches).

Note that when subject and competitor are of equal d.b.h, LP = 1/2 L; and that
LP is inversely related to the influence of competitor on subject tree.

The FORTRAN code necessary to maintain the genetic identity of the subject tree and each of its competitors is quite simple, but, in order to use this information to detect genetic interactions, a measure of influence must be constructed to quantify the relative competitive pressure exerted by competitors of a given genetic identity on a subject tree.

An index of relative influence.--An index of relative influence should provide additional information about the relative influence of a competitor with respect to the other competitors used in constructing a subject tree's polygon. This index should be independent of the area of the polygon itself, because it is desirable to compare relative influence values for different genetic entities across a wide range of local densities. Of the several alternatives considered, the following index appears to satisfy the above objectives:

$$RI_{A/B} = \frac{\sum\limits_{B} (1/LP_j)}{\sum\limits_{i=1}^{j} (1/LP_j)} \qquad (0 <= RI_{A/B} <= 1)$$

where   LP is previously defined, and

$RI_{A/B}$ = relative influence of all competitors from genetic entity B surrounding the subject tree with genetic identity equal to A,

$\sum\limits_{i=1}^{j} (1/LP_j)$ = the sum of the inverse LP distances for all competitors influencing the subject tree, and

$\sum\limits_{B} (1/LP_j)$ = the sum of the inverse distances for all competitors genetic type B influencing the subject tree.

Note that the proposed relative index has the following properties:

1. in a genetic test with a mixture of n genetic entities, there are n relative index values for each subject tree,

2. the sum of all RI values for a given subject tree is always equal to unity,

3. an RI value of zero indicates that no competitors of the given genetic type influenced the subject tree,

4. an RI value of unity indicates that all competitors influencing the subject tree were of the given genetic type, but not necessarily of the same genetic type as the subject tree, and

5. an RI value of unity with the form RA/A indicates a situation in which the subject tree and all of its competitors are of the same genetic type.

It is convenient to refer to polygons of the type referred to in (5) as "pure polygons," as opposed to all others which are "mixed polygons." Figu l illustrates the construction of the APA polygon and the associated relati index.
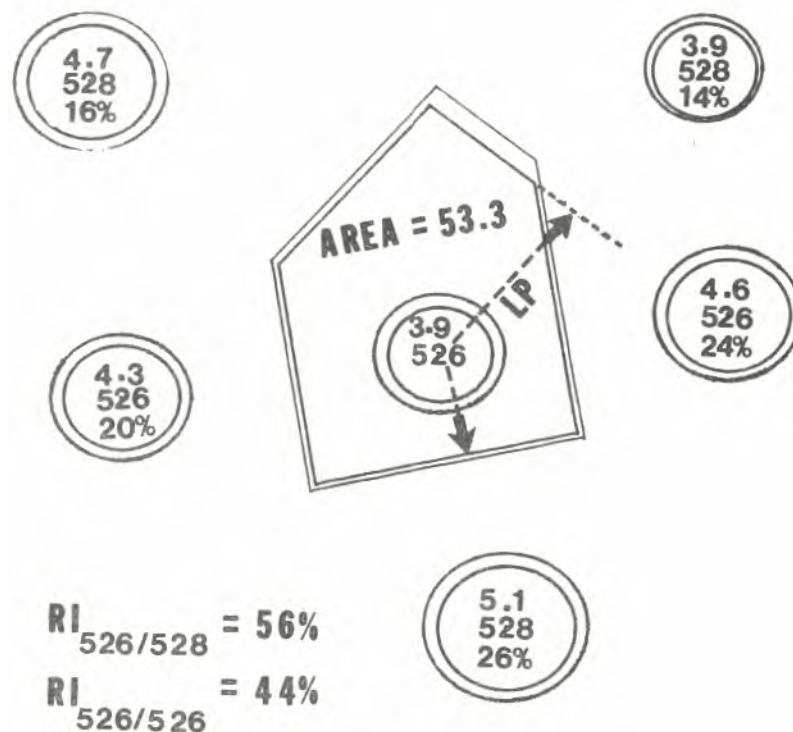

Figure 1.--APA and Relative Influence indices for a typical situation. The inner circles represent diameters at breast height at age 7. In each circle, the top number is the d.b.h. in inches, the middle number is a family I.D., and the lower number is the percent relative influence of the competitor on the subject tree at age 7. The outer circles represent the d.b.h. of each competitor the following year (8). The inner polygon corresponds to year 7, and the outer to year 8.

Regression models to assess response to competition.--Given that APA and RI indices have been computed for each tree in a genetic test, it is then possible to attempt an analysis of the data with the objective of exposing any differences between genetic entities in response to competition. Multiple linear regression models appear to be satisfactory for this objective, at least as a preliminary to more sophisticated (and perhaps more appropriate) methods such as multivariate analyses.

Consider a stand of trees in which individual-tree attributes such as diameters, heights, and crown ratios have been measured for each tree at some initial time (t0). A simple regression model for the prediction of basal area growth of individual trees between time to and some future time tl might appear as follows:

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$$(1) \quad BAG_{t0-t1} = \mu + \beta_1(BAS_{t0}) + \beta_2(HTS_{t0}) + \beta_3(CRS_{t0})$$

where

μ = the mean basal area growth for all trees

BAS_{t0} = the basal area of the subject tree at time t0

HTS_{t0} = the total height of the subject tree at time t0

CRS_{t0} = the ratio of live crown to total height for the subject tree at time t0

and μ, β_1, β_2, and β_3 are least squares coefficients.

This model takes account of the current size and crown development of an individual tree in predicting future growth. Models like this are common in forest growth and yield formulations and perform well in forest stands if the prediction interval (t1-t0) is less than about 5 years. Generally, larger trees with higher crown ratios produce more basal area increment than their smaller counterparts with less crown.

Model 1, even though it might have practical utility, ignores the local density regime experienced by the subject tree. Consideration of APA for the subject tree is added as follows:

$$(2) \quad BAG_{t0-t1} = \mu + \beta_1(BAS_{t0}) + \beta_2(HTS_{t0}) + \beta_3(CRS_{t0}) + \beta_4(APA_{t0})$$

$$= \text{model 1 + APA component}$$

where

APA_{t0} = Area Potentially Available at time t0 for the subject tree (as defined in the previous section), β_4 is a coefficient to be estimated, and

all other terms are previously defined.

The predictive power of the model can now be expected to increase if, indeed, inter-tree competition is a factor in tree growth. Daniels (1981) found this to be the case in his work, noting that APA was the only index powerful enough to add significantly to the prediction of basal area growth in the presence of the other predictors. The coefficient 04 will generally he positive, and represents the average capacity of individual trees to respond to growing space limits imposed by neighbors.

Note that the residuals from prediction in both models 1 and 2 may be related to the tree's genotype as well as interactions with competing trees of other genotypes in the case of mixed plantations.

At this point, allowance is made for mixtures of several genetic entities in a test plantation. The equivalent of model 1 allowing for genetic differences (with t0 and t1 subscripting now dropped for brevity) is:

$$\text{(1A)} \quad \text{BAG} = \mu + \sum_i \alpha_i \lambda_i + \beta_1(\text{BAS}) + \beta_2(\text{HTS}) + \beta_3(\text{CRS})$$

$$+ \beta_{1i}(\text{BAS}_i) + \beta_{2i}(\text{HTS}_i) + \beta_{3i}(\text{CRS}_i)$$

where BAG, BAS, HTS, and CRS were previously defined, and

$\sum \alpha_i \lambda_i$ = a set of indicator variables (λ_i) and their least squares coefficients (α_i),

λ_i = 1 when the subject tree's genetic identity is i and 0 otherwise,

$\text{BAS}_i = \lambda_i(\text{BAS})$, $\text{HTS}_i = \lambda_i(\text{HTS})$, and $\text{CRS}_i = \lambda_i(\text{BAS})$.

As before, β_1, β_2, and β_3 designate the least squares coefficient for the general effect of either BAS, HTS, or CRS on basal area growth for the whole population, and their subscripted counterparts designate specific differences in the response of genetic entity i with respect to the general response. This model is a specialized form of a covariance model in which BAS, HTS, and CRS are the covariates, λ_i are the qualitative design variables (in this case genetic entity), β_1, β_2, and β_3 represent the general regression slope for all trees regardless of genetic origin, and the subscripted coefficients β_{1i}, β_{2i}, and β_{3i} represent specific slopes for each genetic entity. However, unlike many applications of covariance analyses, the goal is not to "adjust" means, but rather to expose genetic differences in terms of the β coefficients associated with variables such as BAS_i, HTS_i, and CRS_i.

Similarly, model 2 can be made sensitive to genetic differences,

$$\text{(2A)} \quad \text{BAG} = \mu + \sum_i \alpha_i \lambda_i + \beta_1(\text{BAS}) + \beta_2(\text{HTS}) + \beta_3(\text{CRS}) + \beta_4(\text{APA})$$

$$+ \beta_{1i}(\text{BAS}_i) + \beta_{2i}(\text{HTS}_i) + \beta_{3i}(\text{CRS}_i) + \beta_{4i}(\text{APA}_i)$$

with the same interpretation, except that APA has been added as an additional predictor. In this model, it is recognized that there is a general relationship between basal area growth (BAG), current tree size (BAS and HTS), crown development (CRS), and competitive status (APA). The goal is to detect any genetic difference in these relationships that would allow a better prediction of future growth knowing the genetic identity of the subject tree; and this sensitivity is provided by the addition of the subscripted terms.

To this point, the genetic identity of surrounding trees has been ignored, which could be a source of error in the models so far presented. The $\text{RI}_{A/B}$ index developed earlier is used to include a general relative influence effect of a genetic entity as a competitor as follows:

$$\text{(3)} \quad \text{BAG} = \mu + \sum_i \alpha_i \lambda_i + \beta_1(\text{BAS}) + \beta_2(\text{HTS}) + \beta_3(\text{CRS}) + \beta_4(\text{APA})$$

$$+ \beta_{1i}(\text{BAS}_i) + \beta_{2i}(\text{HTS}_i) + \beta_{3i}(\text{CRS}_i) + \beta_{4i}(\text{APA}_i)$$

$$+ \sum_j \beta_{5j}(\text{RI.}/j)$$

where

$RI._{\cdot/j}$ = the general relative influence of genetic entity j as competitor (ignoring the genetic identity of the subject tree),

and β_{5j} are least squares coefficients.

The β_{5j}'s are not subscripted by i, reflecting the fact that in this model the genetic identity of the subject tree is ignored, as the goal is to fit a general relative influence effect for each genetic entity as competitor, disregarding the genetic identity of the subject tree. The interpretation of this model is similar to the preceding model 2A, except that now allowance is made for the possibility that genetic entities may not influence the growth of subject trees in the same way. Negative values of β_{5j} indicate a negative influence on the growth of subject trees, positive values a positive influence, and zero (or nonsignificant values) no influence.

As a final genetic refinement to the model, allowance is made for the possibility that specific genetic interactions of subject and competitor could account for some of the variation in the basal area growth of individual trees by the following model:

$$(4) \quad BAG = \mu + \sum_i \alpha_i \lambda_i + \beta_1(BAS) + \beta_2(HTS) + \beta_3(CRS) + \beta_4(APA)$$

$$+ \beta_{1i}(BAS_i) + \beta_{2i}(HTS_i) + \beta_{3i}(CRS_i) + \beta_{4i}(APA_i)$$

$$+ \sum_i \sum_j \beta_{6ij}(RI_{i/j})$$

where the general influence terms (β_{5j}'s) are replaced by specific influence terms (β_{6ij}'s) which account for the genetic identity of both subject and competitor. This form represents an explosion of coefficients, and unless the field test is quite large it may not be possible to fit the model. For example, with only 8 genetic entities, the number of coefficients (prior to restrictions placed to eliminate dependencies) for models 1, 2, 1A, 2A, 3 and 4 are 4, 5, 36, 45, 53, and 109 respectively.

Model 4 appears to be detailed enough to expose genetic differences in density response in even the most complex genetic field tests. To illustrate the application of these methods, they are applied in the next section to a loblolly pine progeny test with a complex structure.

MATERIALS

Seventh- and eighth-year measurements of d.b.h., total height, and length for loblolly pines planted in a Nelder's design [2]/ (Nelder 1962) were used to illustrate the application of the methods developed in the preceding sections. The planting site is in northeast **Mississippi** (Oktibbeha County, 33' 18" North latitude, 88'47" West longitude). Open-pollinated families eight clones in the Weyerhaeuser Company seed orchard at Aliceville, Alabama, are represented in the test. Four of these clones (8-507, 8-509, 8-530, and 8-532) are from ortets in Lamar County, Alabama, two clones (8-505 and 8-519) are from Pickens County, Alabama, and two clones (8-526 and 8-528) are from Greene County, Alabama.

This study used six replicates, with each replication represented by one circular Nelder's Wheel. A wheel consists of 40 measurement spokes,2 border spokes, and 7 planting positions along a spoke. The inside and outside positions are borders, so there are five measurement positions having the following spacings and trees per acre: 6 feet x 6 feet (1210 trees/acre), feet x 6.8 feet (938 trees/acre), 7.7 feet x 7.7 feet (727 trees/acre), 8.8 feet x 8.8 feet (563 trees/acre), and 10 feet x 10 feet (436 trees/acre). Only a single family is planted along a spoke. Families are assigned to adjacent spokes in a particular order to provide competition among trees of only a single family on all sides, competition with trees of the same famil on three sides and with a tree of a different family on the fourth side, an competition with trees of a different family on two sides.

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RESULTS AND DISCUSSION

APA was computed for each non-border tree in the study based on the 7th-year data (Figure 2). Trees exposed by the death of a border tree were treated as border trees in the analysis. The number of competitors influencing each subject tree ranged from 4 to 10, with 5 or 6 being typical. The total number of non-border trees was 1,010; and the number of trees per spoke x family combination ranged from 21 to 30. The means (on a per-tree basis) across all replicates for BAS, HTS, CRS, APA and BAG for each family and position for age 7 appear in Tables 1 and 2 respectively.
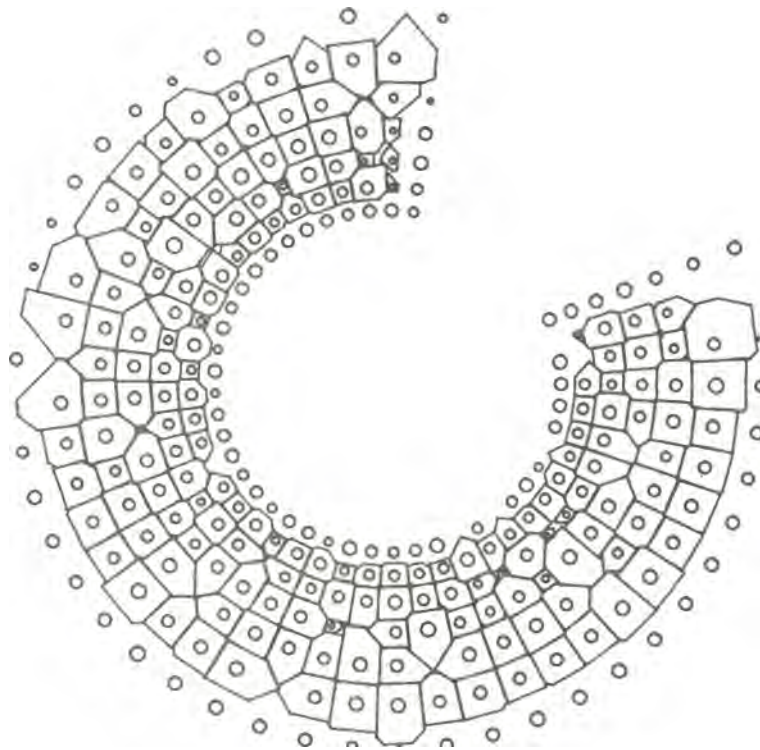

Figure 2.--APA polygons constructed around each non-border tree in one replicate of a Nelders Wheel. The diameters of the circles are proportional to the d.b.h. of living trees.

Table 1.--Means on an individual-tree basis over 6 replications of the Nel Wheels by family at age 7 years

| | FAMILY | | | | | | | |
Variable	505	507	509	519	526	528	530	532
BAS (ft^2)	0.065	0.069	0.053	0.062	0.063	0.066	0.067	0.065
HTS (ft)	18.64	19.29	17.03	18.04	18.92	19.21	19.12	18.84
CRS	0.792	0.801	0.797	0.783	0.808	0.792	0.795	0.798
APA (ft^2)	63.23	70.85	66.23	72.39	70.56	69.87	73.31	73.71
BAG (ft^2)	0.036	0.038	0.036	0.034	0.040	0.036	0.041	0.039

Table 2.--Means on an individual-tree basis over 6 replications of the Nelder's Wheels by density at age 7 years

| | PLANTING DENSITY | | | | |
Variable	1210	938	727	563	436
BAS (ft^2)	0.055	0.060	0.064	0.068	0.071
HTS (ft)	18.86	18.73	18.56	18.60	18.50
CRS	0.761	0.780	0.796	0.820	0.825
APA (ft^2)	35.03	52.20	66.42	87.63	110.56
BAG (ft^2)	0.026	0.030	0.038	0.043	0.051

Relative influence indices were computed according to the procedures given previously. Since there were 8 families, there were 8 RI values per tree, although typically only 1 (a "pure polygon") or two (a "binary polygon" influence values were non-zero. Occasionally 3, but never 4 influence values were non-zero.

Table 3 summarizes the various models as fit to this data set. Any two models in this table can be compared by considering the model with the most terms the "full" model, and the one with the fewer terms the "reduced" model. The following F-test (Neter and Wasserman, 1974) is appropriate for testing the null hypotheis that the coefficients of all the additional terms in the full model are equal to zero:

$$F = \frac{(SSE(R) - SSE(F))/(edf(R)-edf(F))}{SSE(F)/edf(F)}$$

where

    $SSE(R)$ = residual sum of squares for the reduced model
    $SSE(F)$ = residual sum of squares for the full model
    $edf(R)$ = residual degrees of freedom for the reduced model
    $edf(F)$ = residual degrees of freedom for the full model

This test (at the 0.05 probability level) applied to table 3 results in the following, based on the prediction of 7-th year basal area growth:

1. APA by itself is a significant predictor of BAG,

2. BAS, HTS, and CRS are significant predictors of BAG,

3. APA adds significantly to BAS, HTS, and CRS,

4. APA_i adds significantly to BAS, HTS, CRS, and APA, and

5. neither BAS_i , HTS_i, CRS_i, $R_{.}/j$, nor R_i/j add significantly to (4).

Table 3.--Summary of regression models for prediction of 7-th year basal area growth

		Components Included											Residuals		
Mean	λ_i	BAS	HTS	CRS	APA	BAS_i	HTS_i	CRS_i	APA_i	$R_{.}/j$	R_i/j	R^2	SS	d.f.
*					*							0.46	0.159	1008
*		*	*	*								0.35	0.194	1006
*	*	*	*	*	*							0.51	0.145	998
*	*	*	*	*	*				*			0.52	0.142	991
*	*	*	*	*	*	*	*	*	*			0.53	0.140	970
*	*	*	*	*	*				*	*		0.52	0.141	984
*	*	*	*	*	*	*	*	*	*	*		0.53	0.138	963
*	*	*	*	*	*				*		*	0.54	0.136	942

Hence, the only genetic component that contributed significantly to t prediction of basal area growth in this data was APAi, indicating that families differed in their use of growing space for basal area growth. On two APAi coefficients were significant -- those for families 526 and 519. Family 526 had a significant positive coefficient whereas family 519 had a significant negative coefficient. This indicates that trees from family 5 were relatively efficient users of growing space while trees from family 5 were relatively less efficient than trees from the whole population.

An inspection of Table 1 tends to confirm these results. Family 526, which ranked 6th from the top in terms of average basal area per tree across all densities, and also 6th in APA, ranked 2nd in basal area growth per tree. Family 519, which ranked 7th in basal area, but a surprising 3rd in APA, ranked 8th in basal area growth. Interestingly, family 526 also ranked first in crown ratio.

To further investigate the family differences in the relationship of APA to basal area growth, separate simple linear regressions of BAG over APA were fit using data of subject trees from the same family. The results are given in Table 4.

The regression for family 526 not only had the steepest slope relating basal area growth per square foot of APA, but it also had the highest R^2. Also, the regression for family 519 had the smallest slope, but the R2 was relatively low. Because the polygons in each of the above regressions included pure as well as mixed types, the pure cases were separated and fitted also. The results are presented in Table 5.

Table 4.--Simple linear regression coefficients of BAG over APA for mixed and pure polygons combined

Family	No. Obs.	Slope	R^2
505	137	0.27689	0.4377
507	125	0.28528	0.4895
509	124	0.24053	0.3026
519	113	0.23582	0.3121
526	132	0.34866	0.5814
528	127	0.29148	0.4601
530	124	0.27900	0.3840
532	128	0.32896	0.5315

Table 5.--Simple linear regression coefficients of BAG over APA for pure polygons alone

Family	No. Obs.	Slope	R^2
505	24	0.19870	0.4682
507	23	0.35825	0.5641
509	14	0.38807	0.0815
519	17	0.28478	0.5769
526	23	0.39643	0.7235
528	22	0.36406	0.5182
530	18	0.27269	0.3388
532	28	0.35440	0.5854

Here the slopes are generally somewhat steeper and the R^2 values higher. However, the correspondence between the two types is quite close, even though the number of trees involved in the latter regressions is small. These results tend to confirm the lack of interactions between families noted previously.

Although the differences exposed in this analysis are not large, they do illustrate that the methods may have utility in exposing this kind of information in other progeny tests. It should be emphasized that the methods proposed and applied here, even though they appear to be useful, are nonetheless preliminary and require further development. It is especially important to apply the methods to other data sets in which different sets of families are tested under a variety of designs.

Further research in this area may provide at least partial answers to the following questions:

1. Do progenies differ in their ability to respond to competition created by neighboring trees?

2. Is that response conditioned by the genetic makeup of the competitors in addition to size and spatial pattern?

3. What is the heritability of this trait?

4. What is the genetic correlation between this trait and pre-competitive growth rate?

5. How do these traits relate to per acre yield capacity?

6. What is the ideal combination of these two traits for commercial forest production?

7. How do progenies that differ in these traits perform when planted alone? In mixtures with other progenies which differ (and perhaps interact) in one or both of these traits?

8. In short, what changes (if any) should be made in selection, breeding, testing, and deployment of genetic material in light of competition effects?

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